

THE AFFINITIES OF THE CRETACEOUS AMMONITE *NEOSAYNOCERAS* BREISTROFFER, 1947

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ABSTRACT. The cryptic micromorph ammonite *Neosaynoceras* Breistroffer, 1947 is redescribed and shown to be a Cenomanian offshoot of *Salaziceras* Breistroffer, 1936 of the Flickiidae. *Salaziceras* and *Neosaynoceras* are separated from the remaining Flickiidae as Salaziceratinae subfam. nov.

THE Albian–Cenomanian marls of Algeria and Tunisia, Madagascar and Tanzania, and Texas and northern Mexico are well known for their rich faunas of diminutive pyritic ammonites (Pervinquière 1907, 1910; Collignon 1928–1929, 1931, 1964; Böse 1928; Adkins 1928; Young 1979). Some of these are no more than nuclei of larger species, but others are genuinely diminutive, frequently paedomorphic taxa, unknown for reasons of preservational potential or environmental preferences in other facies (Kennedy and Hancock 1971; Kennedy and Wright 1981). The affinities of genera and subgenera *Euhystriocheras* Spath, 1933, *Prionocycloides* Spath, 1925, and *Sakondryella* Collignon, 1964, among these dwarfs, with the Mortoniceratinae were demonstrated by Kennedy and Wright (1981), and the origins of the Flickiidae in Lyelliceratidae by Wright and Kennedy (1979). We deal here with the diminutive and highly distinctive genus *Neosaynoceras* Breistroffer, 1947 (p. 76), type species *Saynoceras gazellae* Pervinquière, 1907 (p. 115, pl. 5, figs. 1–6), which is known only from the lower Cenomanian of Algeria, Tunisia, and Madagascar. The largest known specimens are less than 15 mm in diameter and show modification of ornament suggestive of maturity (crowded sutures, and excentric coiling). When introducing *S. gazellae* in 1907, Pervinquière placed it between *Holcodiscus* Uhlig, 1882 and *Scaphites* Parkinson, 1811 and regarded it as a perisphinctid; Roman (1938, p. 391) concurred with this assignation, but Breistroffer (1947, p. 76) regarded it as a degenerate acanthoceratid. In the *Treatise* Wright (1957, p. 414), following Breistroffer, assigned it to the Acanthoceratinae without comment. It is argued below that *Neosaynoceras* is a Cenomanian offshoot of *Salaziceras* Breistroffer, 1947 of the Flickiidae.

SYSTEMATIC PALAEOLOGY

Repositories of specimens. The following abbreviations are used to indicate the repositories of specimens cited: GPIT—Geologisches und Paläontologisches Institut, Tübingen; OUM—University Museum, Oxford; SP—Collections of the Sorbonne, now in the Université Pierre et Marie Curie, Paris. The Collignon Collection is now housed in the Université de Dijon.

Family FLICKIIDAE Adkins, 1928

Genus *Neosaynoceras* Breistroffer, 1947

Type species. *Saynoceras gazellae* Pervinquière, 1907 p. 115, pl. 5, figs. 1–6, by the original designation of Breistroffer (1947, p. 76).

Diagnosis. Small: largest known specimens less than 15 mm diameter. Phragmocone a globose cadicone, smooth or with faint radial folds and shallow furrows at first which develop into primary ribs with bullate inner and outer ventrolateral tubercles linked across the venter by riblets or striae.

The outer ventrolateral tubercles are opposite or alternate on the venter, more commonly the latter. Body chambers are strongly ribbed and tuberculate and markedly scaphitoid with the inner edge occluding part of the umbilicus; tubercles become spinate and the shell resembles a Horse Chestnut (*Aesculus*) seed case. The suture line is simple with rounded terminations to the constituent elements of lobes and saddles; E/L is narrow and asymmetrically bifid, L broad with few incisions, L/U₂ small and little subdivided.

Discussion. Few genera resemble *Neosaynoceras*, and this is a major factor in the difficulty experienced in deciding its affinities. The most obvious comparison is with the Scaphitaceae, especially given the obviously scaphitoid coiling of the body chamber of some specimens (Pl. 21, figs. 1, 4, 20) and the looping of ribs between outer ventrolateral tubercles (Pl. 21, figs. 3, 12), a style of ornament shown by several *Scaphites* (e.g. Wiedmann 1965, pl. 57, figs. 1–7) of essentially the same date. The test of scaphitid affinities lies in the suture line. Scaphitids have quadrilobate early sutures, after a quinquilobate primary suture (see Doguzhaeva and Mikhailova 1982) and also 'pseudolobes' in the saddle L/U, resulting from the widening of this saddle and the deepening of its central lobule (Wiedmann 1965; Kullman and Wiedmann 1970). Unfortunately the preservation of the Madagascar material of *Neosaynoceras gazellae* available to us has not allowed the exposure of the early sutures. The mature suture lines, however, show no trace of development of 'pseudolobes', which are manifest in contemporary Scaphitaceae. Consequently we dismiss the idea of affinities with this group, despite the scaphitoid body chambers.

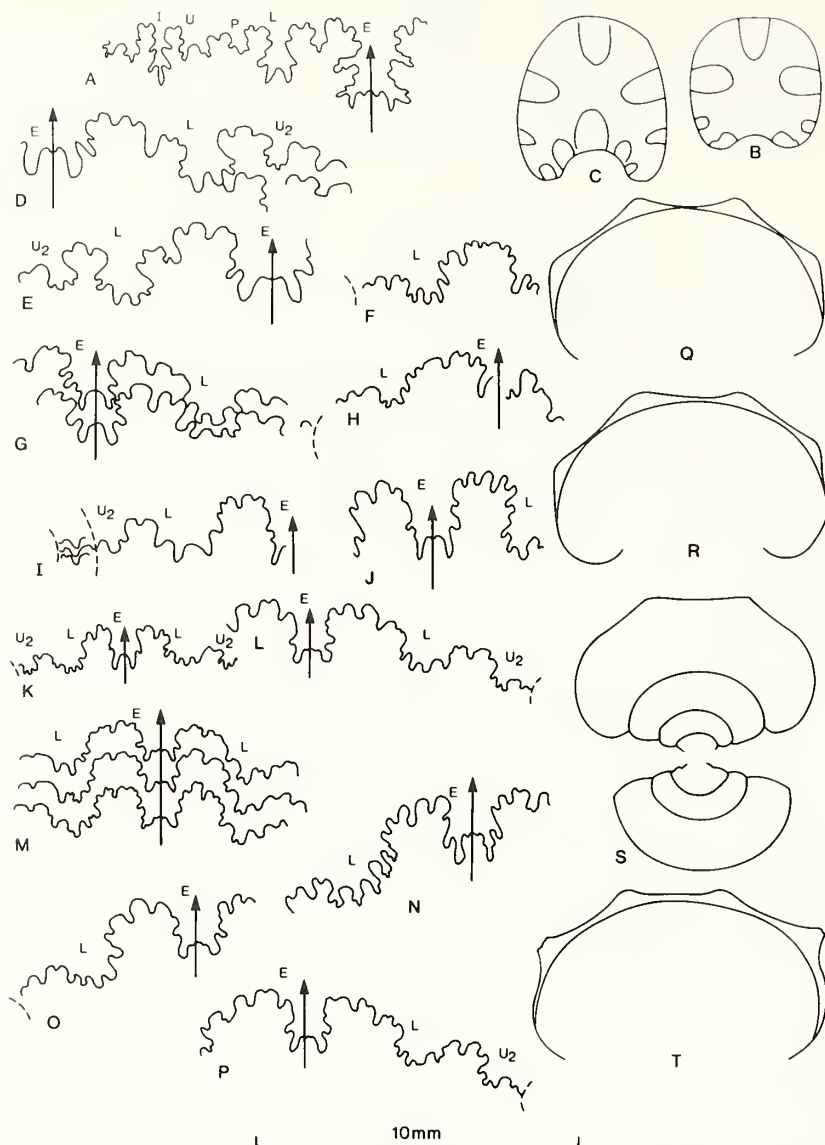
Affinity with the Acanthoceratidae is suggested because these are the only contemporary group in which strong ventrolateral tuberculation commonly develops, as in lower Cenomanian genera *Mantelliceras* Hyatt, 1903, *Sharpeiceras* Hyatt, 1903, and *Graysonites* Young, 1958 of the Mantelliceratinae, or *Acompsoceras* Hyatt, 1903 of the Acanthoceratinae. Study of the early development of these taxa shows that their early ontogeny (well shown in similarly sized specimens figured by Pervinquière 1907, 1910 and Collignon 1928–1929, 1931) involves early acquisition of umbilical, inner, and outer ventrolateral tubercles, plus in some lateral or even siphonal tubercles (e.g. *Acompsoceras*), and ribs at a stage where *Neosaynoceras* is almost smooth. These early Cenomanian acanthoceratids also lack constrictions or furrows and looping of ribs between ventral tubercles.

The closest analogues to *Neosaynoceras* lie in the late Albian *Salaziceras* Breistroffer, 1936 (p. 64, type species *Ammonites salazacensis* Hébert and Munier-Chalmas, 1875, p. 114, pl. 5, fig. 6). Scholz (1979) illustrates the ontogeny of the genus in detail and, although the taxonomic treatment may be questioned, specimens named *Salaziceras salazacense peyrolasense* Scholz, 1979 (p. 93, pl. 21, figs. 16, 18–20; text-figs. 25, 26B, 27C–G, K, N–Q) have nuclei with furrows and folds like those of *Neosaynoceras* nuclei (e.g. Scholz 1979, pl. 21, figs. 18–20), while specimens described as *Salaziceras breistrofferi pseudonodosa* Scholz, 1979 (p. 96, pl. 21, figs. 23, 24, 26; text-fig. 27R) develop a single ventral tubercle linked across the venter by a looped rib (text-fig. 10–Q). Scholz also introduced a subgenus *Salaziceras* (*Noskytes*) Scholz, 1979, type species *S. (N.) bakonyense* Scholz, 1979 (p. 97, pl. 22, figs. 1–5; text-figs. 27S, 28) for species with a transient juvenile stage with siphonal tubercles and an adult body chamber with strong ventral tubercles linked across the venter by looped ribs (text-fig. 1G–H, K–N, R–S), the adult aperture developing a remarkable constriction and ventral rostrum (text-fig. 1H, L, M). Examination of casts of the types of *S. (N.) bakonyense* throws doubt on the existence of a true siphonal tubercle. In one paratype it is displaced from the siphonal line, while in the other it is visible on a few ribs only and is likely to be a malformation.

It also appears possible that *Noskytes*, which has a highly specialized aperture, is the microconch of *Salaziceras*. In any case, the common morphological features of these tuberculate upper Albian *Salaziceras* and lower Cenomanian *Neosaynoceras* suggest close affinity, and that *Neosaynoceras* is a descendant of *Salaziceras* in which the single ventrolateral tubercle of *S. breistrofferi pseudonodosa* and of '*Noskytes*' body chambers has been replaced by inner and outer ventrolateral tubercles. The suture lines of both genera are simplified, but this is no strong indicator of affinity, rather reflecting their small size.



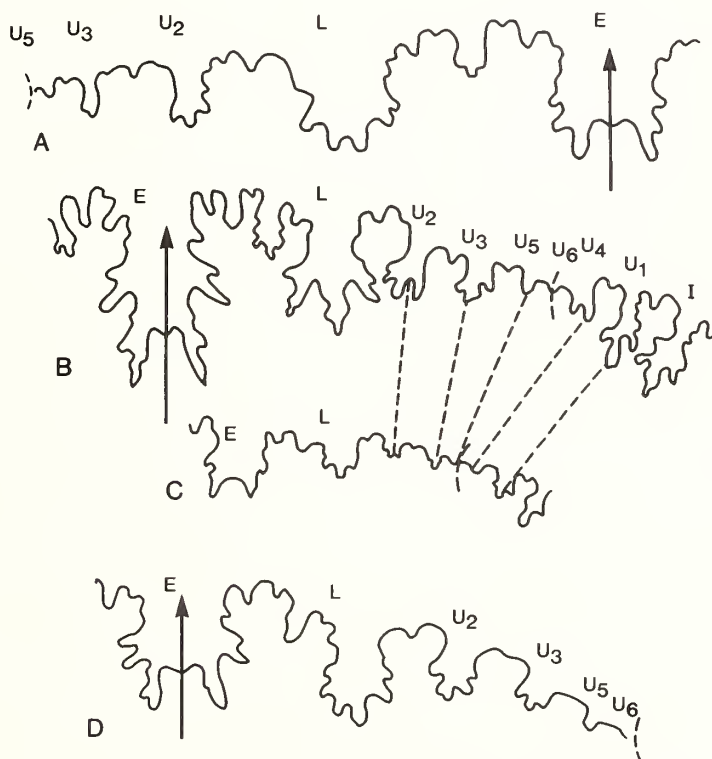
TEXT-FIG. 1. A–D, *Metascaphites thomasi* (Pervinquière, 1907), holotype, the original of Pervinquière 1907, pl. 4, figs. 30, 31, from Djebel Mrhila, Tunisia. Sorbonne Collections, now in the Université Pierre et Marie Curie, Paris. E–F, *M. thomasi* (Pervinquière, 1907), GPIT 1486/243, the original of Scholz 1979, pl. 22, fig. 6. G–H, K–N, R–S, *Salazicerus* ('*Noskytes*') *bakonyense* Scholz, 1979. G–H, GPIT 1426/240, a paratype, the original of Scholz 1979, pl. 22, fig. 3; K–M, GPIT 1486/238, a paratype, the original of Scholz 1979, pl. 22, fig. 1; N, GPIT 1486/241, inner whorls of the holotype, the original of Scholz 1979, pl. 22, fig. 4; R–S, GPIT 1486/242, a paratype, the original of Scholz 1979, pl. 22, fig. 5. I–J, T–U, *S. (S.) breistrofferi breistrofferi* Scholz, 1979. I–J, GPIT 1486/237, a paratype, the original of Scholz 1979, pl. 21, fig. 28; T–U, GPIT 1486/236, the original of Scholz 1979, pl. 21, fig. 27. O–Q, *S. (S.) breistrofferi pseudonodosa* Scholz, 1979, GPIT 1486/235, a paratype, the original of Scholz 1979, pl. 21, fig. 26. The originals of E–U are from the upper Albian of the Bakony Mountains, Hungary. All figures are $\times 2$.



TEXT-FIG. 2. Suture lines and whorl sections. A-B, *Metascaphites subthomasi* Wiedmann, 1962, GPIT Ce 1162/76, holotype, the original of Wiedmann 1962, pl. 13, fig. 8, text-figs. 57, 58, from the upper Albian of Izurdiaga, Navarra, Spain. C, *Scaphites (Scaphites) peroni* var. *inornata* Pervinqui re, 1910, the original of Pervinqui re 1910, pl. 2, fig. 15, from Berrouaghia, Algeria. Sorbonne Collections, now in the Universit  Pierre et Marie Curie, Paris. D, E, *M. thomasi* (Pervinqui re, 1907), holotype, the original of Pervinqui re 1907, pl. 4, figs. 30, 31, from Djebel Mrhila, Tunisia. Repository as for C. F-T, *Neosaynoceras gazellae* (Pervinqui re, 1907). F, the lectotype, the original of Pervinqui re 1907, pl. 5, fig. 2, from Pont du Fahs, Tunisia; G, T, the original of Pervinqui re 1907, pl. 5, fig. 4; H, the original of fig. 6, both from Guern er Rhezal, Tunisia. Repository as for C. I, OUM KX1604; J, OUM KX1614; K, OUM KX1611; L, P, Q, OUM KX1609; M, OUM KX1606; N, R, OUM KX1610; O, OUM KX1607; S, OUM KX1613. All specimens from the lower Cenomanian of Beraketa-sur-Sakondry (Manera), Madagascar.

A further diminutive taxon with ventral tubercles is *Metascaphites* Wiedmann, 1962 (p. 212), proposed as a subgenus of *Scaphites*, with *Scaphites?* *thomasi* Pervinqui re, 1907 (p. 121, pl. 4, figs. 30, 31; text-fig. 39) as type species. The holotype by monotypy, and a specimen from the upper Albian of Hungary, are shown in text-fig. 1A–F. When introducing this genus, Wiedmann also included a second species *Metascaphites subthomasi* Wiedmann, 1962 (p. 218, pl. 13, fig. 8; text-figs. 57, 58) for a fragment of only three camerae from the mid-upper Albian of Irzudiaga, Navarra, Spain. *M. subthomasi* has a basically quadrilobate suture with well-developed ‘pseudolobe’ (text-fig. 2A) and is a scaphitid. In contrast, *M. thomasi* shows only a part of the external suture (text-fig. 2D, E), which complements that of the other known specimen (text-fig. 3D) from Hungary. These closely recall the sutures of *Salaziceras* (*Salaziceras*) and *S.* (*Noskytes*), and indeed Scholz included *M. subthomasi* in *Noskytes*. This is nomenclatorially irregular, and those who believe *Noskytes noskensis* and *M. thomasi* to be congeneric must use the latter generic name, which has priority. The Spanish *M. subthomasi* is a *Scaphites* allied to *Scaphites peroni* Pervinqui re, 1910 (p. 26, pl. 2, figs. 10–16), especially the variety *inornata* which has a similar whorl section and suture. Irrespective of the relationship between *Noskytes* and *Metascaphites*, the latter is easily separated from *Neosaynoceras* by its possession of only one row of ventrolateral tubercles.

Occurrence. Lower Cenomanian of Algeria, Tunisia, and Madagascar.



TEXT-FIG. 3. Sutures. A, *Salaziceras* (*Salaziceras*) *salazacense* (H bert and Munier-Chalmers, 1875) at a whorl height of 8.7 mm. B, C, *S.* (*'Noskytes'*) *bakonyense* Scholz, 1979. B at a whorl height of 5.5 mm; C at 2 mm. D, *Metascaphites thomasi* (Pervinqui re, 1907) at a whorl height of 8 mm. A–D are copies of Scholz (1979, text-figs. 27B, sb, sa, t).

Neosaynoceras gazellae (Pervinquier, 1907)

Plate 21, figs. 1–22; text-fig. 2F–T

- 1907 *Saynoceras gazellae* Pervinquier, p. 115, pl. 5, figs. 1–6.
 1925 *Saynoceras gazellae* Pervinquier; Diener, p. 96.
 1931 *Saynoceras gazellae* Pervinquier; Collignon, p. 77 (37).
 1938 *Saynoceras gazellae* Pervinquier; Roman, p. 391.
 1947 *Neosaynoceras gazellae* (Pervinquier); Breistroffer, p. 92 (76).
 1947 *Neosaynoceras gazellae* (Pervinquier) var. *globosa* Breistroffer, p. 92 (76).
 1957 *Neosaynoceras gazellae* (Pervinquier); Wright, p. L414, fig. 534: 1a, b.
 1964 *Neosaynoceras gazellae* (Pervinquier); Collignon, p. 26, pl. 323, figs. 1430–1432.

Types. Pervinquier (1907, p. 115) based this species on eight specimens, of which three were figured. We have traced four of these in the Collections of the Sorbonne, Paris (now housed in the Université Pierre et Marie Curie, Paris), including the lectotype designated by Breistroffer (1947, p. 76) (the original of Pervinquier 1907, pl. 5, figs. 2a, b, 3) and the holotype of var. *globosa* Breistroffer (1947, p. 76) (the original of Pervinquier 1907, pl. 5, figs. 4a–c, 5a, b) from the lower Cenomanian of Pont du Fahs and Guern er Rhezal, Tunisia.

Other specimens studied. More than a hundred specimens from the lower Cenomanian of Beraketa-sur-Sakondry, Madagascar, including the originals of Collignon (1964, pl. 323, figs. 1430–1432).

Description. The smallest specimens we have seen are 4.5 mm in diameter. At this size, the shell is a globose cadicone, with a deep conical umbilicus and very depressed whorls, the whorl breadth to height ratio ranging from 1.56 to 1.73. The umbilical wall slopes outwards, with a rounded shoulder and very broad, rounded venter. Moulds are either smooth or bear low radial folds from a diameter of 3–4 mm onwards; these are stronger on the flank, but weaken and may disappear on the venter. Some specimens also bear occasional shallow transverse furrows or constrictions. As size increases, the lateral folds strengthen progressively, and develop into distinct ribs (Pl. 21, figs. 15, 17) of which there may be up to sixteen per whorl in the largest specimens, although there is wide variation (Pl. 21). As the ribs strengthen, inner and outer ventrolateral tubercles develop, elongated parallel to the ribs and generally blunt. There is again wide variation in the relative development of both tubercles and ribs. In general, the outer ventrolateral tubercles are slightly offset and linked across the venter by low riblets or striae (Pl. 21, figs. 3, 12), which either loop or occasionally zigzag between them.

Few specimens have any part of the adult body chamber preserved but, of those that do, most show sutural crowding at a phragmocone diameter of 7–9 mm, with a single Madagascar example septate at 14 mm diameter. At this diameter, ribs are well developed for the preceding whorl and tubercles for the preceding quarter of a whorl (generally from 6 to 7 mm onwards) (Pl. 21, figs. 14, 18). The whorl section remains depressed at the end of the phragmocone with a whorl breadth to height ratio of 1.47 to 1.89, but it becomes markedly polygonal in costal section as a result of the development of ribs and tubercles (Pl. 21, figs. 2, 16).

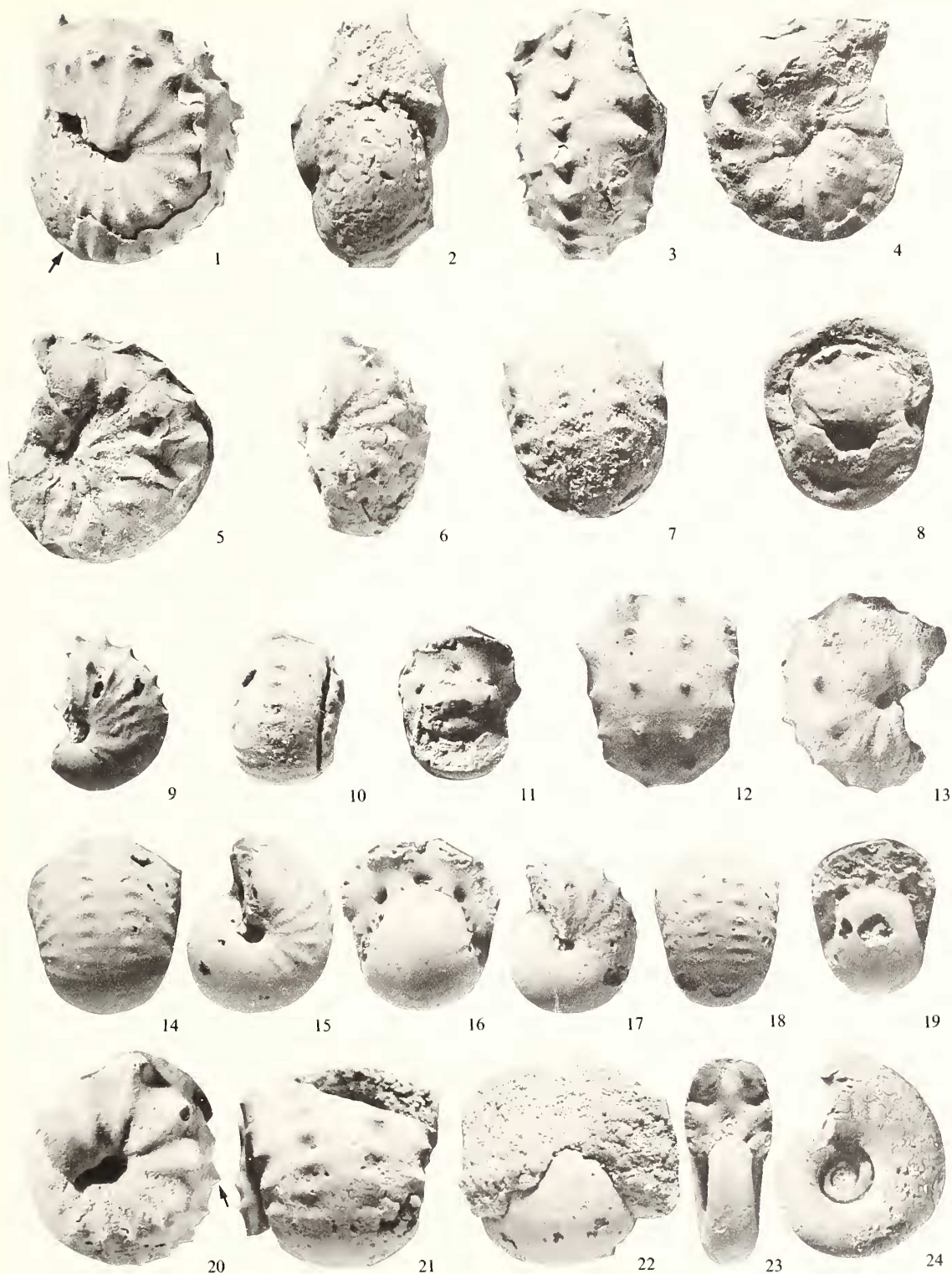
Body chambers have been seen to extend for up to two-thirds of a whorl, but none is complete. Coiling becomes markedly scaphitoid (Pl. 21, figs. 1, 4, 20) with the umbilicus partly occluded; the body chambers have

EXPLANATION OF PLATE 21

Figs. 1–22. *Neosaynoceras gazellae* (Pervinquier, 1907). 1–3, lectotype, the original of Pervinquier 1907, pl. 5, figs. 2, 3; 4, 5, paralectotype, the original of Pervinquier 1907, pl. 5, fig. 1; 6–8, paralectotype, the original of Pervinquier 1907, pl. 5, figs. 4, 5; 9–11, paralectotype, the original of Pervinquier 1907, pl. 5, fig. 6. 1–3, from Pont du Fahs, Tunisia; 4–11, from Guern er Rhezal, Tunisia. All specimens are from the Sorbonne Collections, now in the Université Pierre et Marie Curie, Paris. 12, 13, OUM KX1608; 14–16, the original of Collignon 1964, pl. 323, fig. 1430; 17–19, the original of Collignon 1964, pl. 323, fig. 1431; 20–22, the original of Collignon 1964, pl. 323, fig. 1432. 12–22, from Beraketa-sur-Sakondry (Manera), Madagascar.

Figs. 23, 24. *Scaphites* (*Scaphites*) *peroni* var. *inornata* Pervinquier, 1910, the original of Pervinquier 1910, pl. 2, fig. 15, from Berrouaghia, Algeria. Repository as for figs. 1–11.

All figures $\times 3$. Arrows indicate where septation ceases.



flattened sides; the section remains depressed (whorl breadth to height ratio up to 1.8) and polygonal. Tubercles strengthen into finger-like spines (Pl. 21, fig. 2), ventral and ventrolateral ribbing declines, and the mould resembles a miniature Horse Chestnut seed case.

Typical suture lines are shown in text-fig. 2F–P. Although there is variation in detail, E is broad with a large median element, and E/L broad and asymmetrically bifid with a large incision adjacent to L. L is broad and shallow with more or less uniform simple lobules, and L/U smaller, simple, and bifid. The preservation precludes development of I, but septal faces (Pl. 21, fig. 16) show it to have been narrow.

Discussion. The generic discussion outlines features which differentiate *N. gazellae* from the most closely comparable species of *Salazicerias*, *Noskytes*, and *Metascaphites*. Separation of inflated forms as var. *globosa* Breistroffer, 1947 is unnecessary. *Saynoceras boulei* Collignon, 1931 (p. 76 (36), pl. 7 (3), fig. 22) is probably not a species of *Neosaynoceras*. It differs from *N. gazellae* in having relatively well-developed umbilical tubercles which give rise to single or paired ribs with conical inner ventrolateral tubercles, three times as numerous as the umbilical and feeble outer ventrolateral tubercles that disappear on the body chamber, with occasional siphonal tubercles on a siphonal ridge. These all suggest that it is an acanthoceratine, perhaps allied to some species of *Protacanthoceras*, e.g. *P. arkelli* Wright and Kennedy, 1980 (figs. 24–26) or *P. proteus* Wright and Kennedy, 1980 (figs. 50, 52).

Occurrence. Lower Cenomanian pelagic marl facies of Algeria, Tunisia, and Madagascar.

DISCUSSION

Wright and Kennedy (1979) included *Salazicerias* in Flickiidae, since there was good evidence of a phyletic line from *Salazicerias* to *Ficheuria* and thence to the rest of the family, and since *Salazicerias* was already a dwarf form with simplifying suture line. Scholz's (1979) demonstration of the morphological range within *Salazicerias* and the present linking of *Neosaynoceras* to *Salazicerias* shows that within Flickiidae there were two trends: one to forms with smooth shells and simple sutures, the other to strongly ornamented forms with tuberculate venters and more normal sutures. It is reasonable to distinguish these as subfamilies and we therefore group *Salazicerias* (including *Noskytes* and *Metascaphites*) and *Neosaynoceras* in Salaziceratinae subfam. nov., distinguished by strong ornament and normally frilled sutures, leaving *Ficheuria*, *Flickia*, and *Adkinsia* in Flickiinae *sensu stricto*.

Acknowledgements. We thank Dr. D. Pajaud of the Université Pierre et Marie Curie, Paris, for allowing us access to the Pervinquière Collection, and the late General M. Collignon of Moirans, Isère, for the loan of his collection of Madagascar *Neosaynoceras*. The technical assistance of the staff of the Geological Collections, University Museum, Oxford, is gratefully acknowledged, as is the financial assistance of the Natural Environment Research Council and Wolfson College, Oxford.

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Typescript received 19 January 1983

Revised typescript received 4 May 1983